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HIGHLIGHTS

• Visual stimuli induce an early phase-locked Mu-rhythm in the sensorimotor cortex which is task-dependent.

• Visual stimuli can induce a persistent decrease of non-phase-locked Mu-rhythm.

• Mu-rhythm can both inhibit and promote information processing in the sensorimotor cortex.

ABSTRACT

Objective: The Mu-rhythm has been proposed as both an inhibitor ("idling hypothesis") and as a promoter ("processing hypothesis") of information processing in the primary sensory-motor cortex (SM-C). We tested these possibilities by analyzing the phase-locked and non-phase-locked Mu response during the execution of a visual-motor task.

Methods: EEG was recorded in 13 subjects during the visual presentation of an arrow which indicated the direction of the finger motion to be executed after the presentation of a second stimulus. The EEG activity in the α -range (Mu- α) and β -range was evaluated by a method which segregated the phase-locked and the non-phase-locked response. The event-related Mu-response observed during this task was compared with that computed when the subjects saw the same arrow-stimuli but did not perform any task (passive test).

Results: Visual stimuli induced a phase-locked α -oscillation which began \approx 50 ms after the stimulus onset and persisted for about 150–200 ms. This response was much higher when stimuli were used for motion planning than when they were passively observed, and was more marked in the α -range than in the β -range. The phase-locked response was followed by a persistent decrease of the non-phase-locked Mu-activity similar to that previously reported with the event-related desynchronization/synchronization method.

Conclusions: The Mu-wave is not a single phenomenon. It was segregated here into two components, one with an early and short-lasting phase locked-response to visual stimuli, which increased during the task execution, and the other without phase-locked responses which persistently decreased during the task execution.

Significance: Present data suggest that Mu-activity performs a double action, increasing the information processing of one task (according to the "processing hypothesis") and decreasing the computation of other potentially interfering tasks (according to the "idling hypothesis"), with task selection being achieved by choosing their phase-association to the Mu-wave.

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1. Introduction

The Mu rhythm consists of short-lasting (0.5-2 s) electroencephalographic (EEG) oscillations in the alpha range (8-12 Hz):

 $Mu-\alpha$) recorded from the primary sensorimotor cortex (SM-C) at rest (Pineda, 2005; Muthukumaraswamy and Johnson, 2004; Pfurtscheller and Lopes da Silva, 1999). Although the Mu rhythm was first reported more than 50 years ago (Chatrian et al., 1959; Gastaut and Bert, 1954; Penfield, 1954), it has been studied less than other cortical oscillations because it was initially observed in only a small percentage of the population (Koshino and Isaki, 1986), a fact that changed with the development of new EEG methods (Makeig et al., 2002).





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The physiological function of the Mu-rhythm is still unknown. Because the Mu-rhythm is attenuated by voluntary movement (Babiloni et al., 1999; Salenius et al., 1997; Leocani et al., 2001; Salmelin and Hari, 1994b) and somatosensory stimulation (Salenius et al., 1997), it was initially considered as an "idling" or "nil-work" rhythm which reflected a SM-C inhibition similar to that proposed for occipital alpha waves and vision (idling hypothesis; IH) (Kuhlman, 1978; Pfurtscheller et al., 1996). However, there is also data showing a Mu-rhythm enhancement during the execution of tasks involving, for example, attentive expectation, working memory or short-term memory (Klimesch et al., 1999; Krause et al., 2000), data which suggest that Mu-rhythm facilitates the information processing (processing hypothesis; PH) (Basar et al., 2000, 2001; Linkenkaer-Hansen et al., 2004; Palva and Palva, 2007). The relative relevance of the apparently antagonistic activities ("idling" vs. "processing" function) of Mu rhythm is still a matter for debate.

The initial assumption that Mu-rhythm is exclusively modulated by movements (Gastaut and Bert, 1954; Chatrian et al., 1959) is presently under revision. It has been reported that the Mu-rhythm amplitude can change with somatosensory (Muthukumaraswamy and Johnson, 2004; Muthukumaraswamy et al., 2004) and visual (Koshino and Niedermeyer, 1975; Pfurtscheller, 1992; Pfurtscheller and Lopes da Silva, 1999; Muthukumaraswamy and Johnson, 2004; Cheng et al., 2008) stimulation. This, and the change of Mu-rhythm observed during motor planning (Pfurtscheller and Berghold, 1989; Pfurtscheller et al., 2006), a task which involves the SM-C (Rodriguez et al., 2004), have suggested that the Mu-rhythm is a link between vision and action, translating "seeing" of occipital cortex (α -wave) into "understanding" of SM-C (Pineda, 2005).

The possible involvement of the Mu-rhythm in the early processing of visual information with an event-related paradigm was studied here. Our initial hypothesis was that visual stimuli modify Mu rhythm particularly when they are being used to generate motor planning. Although the Mu-rhythm is basically considered as an oscillation in the alpha range, the existence of a second band in the beta range (13–24 Hz) has also been suggested (Pineda, 2005; Muthukumaraswamy and Johnson, 2004; Pfurtscheller and Lopes da Silva, 1999; Hari et al., 1998; Engel and Fries, 2010). Thus, both alpha (Mu- α) and beta (β) oscillations were considered here.

2. Material and methods

A total of 13 volunteers ranging between 24–38 years of age were studied. All subjects were in good health, had no prior history of cerebral disease or medical treatment which might influence motor performance, and had adequate cognitive and visual-motor functions to perform the test. All subjects were right-handed according to the Edinburgh Inventory of handedness (Oldfield, 1971). The study was approved by the local Research Ethics Committee.

2.1. Procedure

Tests were performed with the right hand in a sound-attenuated and temperature regulated $(22 \pm 1 \,^{\circ}\text{C})$ room which was lit by homogeneous white light and that provided stable and reproducible environmental conditions. During the experiments, the subjects were sitting comfortably in a chair in front of a computer screen (60 mm) which showed the visual stimuli (Eevoke, ANT Software, Enschede, The Netherlands).

Two tests were conducted. In the active test, two successive visual stimuli were displayed, a first stimulus (an arrow) indicating

the direction of the finger motion to be performed when a second stimulus (a circle) gave the signal to execute the movement. In the passive test, the subjects saw the same stimuli but no tasks were performed. Only the Mu-response to the first stimulus was evaluated here (motor response started \approx 2000 ms after the first stimulus and \approx 400 ms after the second stimulus). In other words, the active test consisted of preparing to move the thumb in a direction which depended on the instruction given by the first stimulus (a red arrow pointing up-down-right-left). The thumb movement could not be initiated until a large red dot (second stimulus) replaced the first stimulus on the computer screen. The study consisted of 100 event-related trials separated by rest intervals. The instructions to the subjects used in the active test were: "please, move your thumb (initially placed on a central point of a joystick) to press the button located above, below, to the right or to the left of your thumb (30 mm from the central button), and return your thumb to the initial position as fast as possible. In each trial, the specific button to be pressed will be indicated by the direction of the arrow on the screen, but do not move until the arrow changes into a large red dot". A joystick was used for this task. At the beginning of the task, the tip of the right-thumb was touching a button located exactly in the middle of the four surrounding buttons serving as the targets of the movements. The task of the passive test consisted of watching the same stimuli but doing nothing with them (the tip of the right-thumb continued to touch the middle button). In the active test, the shape of the first stimulus (an arrow pointing in a specific direction) identified the direction of the movement to be executed later, whereas the appearance of the second stimulus (a solid dot) signalled the execution of the previously prepared movement. So, after the first stimulus the subjects needed to identify the direction of the arrow stimulus, to link the analyzed stimulus with a motor task (visual-motor executive function), and to wait for a second stimulus. In the passive test, the characteristics of the stimuli had no practical consequences on behavior, with the right-thumb remaining motionless after the stimuli observation.

In both tests, subjects were instructed to rest between trials (7 s) looking at the computer screen which was switched off for the first 4 s (spontaneous movements such as those used to prevent weariness or irritation of eyes were then allowed) and then the screen was switched on for the last 3 ± 1.2 s and displayed a central white circumference which was used to fix the eyes before beginning the task. Thus, the time intervals for each test were 4 s for the initial resting period, 3 ± 1.2 s for the eye-fixing period, 1.6 s for the arrow stimulus, and 0.6 s for the dot stimulus. All visual stimuli were the same size (20 mm diameter).

2.2. Acquisition and analysis of EEG

EEG data were recorded with Ag/AgCl electrodes (electrode impedance lower than 10 K Ω), using AMP-TRF136AB amplifier and the ASA software (both of ANT, Enschede, The Netherlands). EEG data were digitized (at a rate of 512 Hz/channel) from 128 electrodes placed according to the extended International 10–20 system and referenced to the ear (Oostenveld and Praamstra, 2001). Thumb movements were monitored with an accelerometer located in the dorsal portion of the proximal phalanx of the thumb (Model 7290A-2; Microtron, Endevco; USA) and with a surface electrode which recorded electromyographic activity of the pollicis brevis muscle (digitized at 2000 Hz).

Although the Mu rhythm basically consists of oscillations in the alpha range (8–12 Hz: Mu- α), the existence of a second band in the beta range (13–24 Hz) has been also suggested (Pineda, 2005; Muthukumaraswamy and Johnson, 2004; Pfurtscheller and Lopes da Silva, 1999; Hari et al., 1998). Therefore, we evaluated here oscillations in both the alpha (Mu- α) and the beta (β) range. The

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